

THE REPRODUCTIVE PHYSIOLOGY OF THE INTERTIDAL
PROSOBRANCH *THAIS LAMELLOSA* (GMELIN). I.
SEASONAL CHANGES IN THE RATE OF
OXYGEN CONSUMPTION AND BODY
COMPONENT INDEXES ¹

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There have been many methods used to determine the course of the annual reproductive cycle of marine invertebrates (Giese, 1959). Spawning, numbers of larvae, the appearance of ripe gametes in gonads, the brooding of eggs, and the relative size of gonads and other body components have been used by different investigators to define the reproductive season. Giese (1969) has reviewed the available literature on the use of the body component index approach to studying seasonal changes in the relative size of the body components and on the biochemical composition of each component of molluscs.

The only papers which have been published on seasonal changes in body component indexes of gastropods have dealt with the broadcast fertilizing abalones. Boolootian, Farmanfarmanian and Giese (1962) used cross sectional area to follow seasonal changes in the gonad and hepatic indexes of two species of abalone, *Haliotis cracherodii* and *H. rufescens*. They found an inverse relationship between seasonal changes in the size of the gonad and the hepatic gland. Webber and Giese (1969) determined seasonal index changes in the gonad weight of *H. cracherodii* and found a seasonal periodicity in its size. Maximal gonad growth occurred during the summer months just prior to spawning in early fall. Webber (1970) extended the body component analysis of this species to include the digestive tissue and foot and found two periods of rapid gonadal growth, one prior to spawning and a second just after it. The size of the foot decreased during the first (larger) period of gonadal growth, but increased during the second (smaller) period. He found the size of the digestive gland to change little during the reproductive cycle.

Giese (1969) presented body component index data from single collections of three species: the black abalone *Haliotis cracherodii*, the keyhole limpet *Megathura crenulata*, and the moon snail *Polinices lewisii*. He found a wide difference in the shell indexes, ranging from 7.4% for *M. crenulata*, to 37% for *H. cracherodii*, to 61.6% for *P. lewisii*. The foot was the dominant soft part in all three species.

This paper reports the results of an investigation of *Thais lamellosa* (Gmelin) which is a carnivorous neogastropod snail of the west coast of North America. Its diet usually consists of the barnacles *Balanus cariosus* and *B. glandula* (Connell, 1960, 1970; Emlen, 1966). The species can also feed on the mussels *Mytilus*

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edulis and *M. californianus*. Male and female *T. lamellosa* aggregate to breed between October and June and aggregation is completed in one to three months in the Puget Sound area (Spight, 1972). Fertilized eggs are enclosed in capsules which are attached to rocks. The number of eggs and capsules produced per female is proportional to its size (Emlen, 1966; Spight, 1972). One population which Spight studied was located in the same vicinity as the one investigated by this author.

Nutrient deposition or depletion is dependent upon the balance between anabolism and catabolism. One measure of metabolic activity often used is the rate of oxygen consumption which is affected by factors that fluctuate seasonally such as food availability and water temperature. Changes in the metabolic rate of a species affect metabolite accumulation or depletion.

METHODS AND MATERIALS

Adult (> 32 mm long) specimens of *T. lamellosa* were collected either intertidally or with scuba gear at approximately monthly intervals from Turn Island, Washington and immediately taken to the Friday Harbor Laboratories. Snails were placed in an aquarium of flowing sea water along with specimens of *Balanus cariosus* which served as food. Surface water temperature was measured at the time of each collection.

Freshly laid egg capsules were collected at Turn Island on January 19, 1969. Capsules were dried to constant weight by lyophilization and weighed individually.

Respiratory rates

Standard Warburg techniques at 10° C and 30‰ salinity with the modifications of Duerr (1967), were used to determine the rate of oxygen consumption for a 24 hour period as soon as possible after the animals had been collected. After removal from the respirometer, animals were dried, numbered, frozen, and stored for further analyses.

Component indexes

Animals were removed from the freezer, the shell and foot wiped dry, and the animals were weighed. This weight was the animal's entire weight. The shell and operculum were removed, the animals were sexed, and then dissected into foot and visceral mass. The plane of dissection was from just in front of the tentacles to the posterior edge of the opercular scar. Excess water was wiped from the foot and visceral mass, and the components were immediately frozen between two cakes of dry ice. The frozen components were then weighed and immediately lyophilized. The foot and visceral mass were dried to constant weight, weighed separately, and stored over calcium chloride or in a freezer until chemical analyses could be made. Each animal was thus divided into four components: shell, body water, visceral mass, and foot.

Giese's definition of the body component index (1959, 1969) has been modified in this paper so that each body component index, except that of body water, is given as dry weight of the component ($\times 100$) divided by the entire weight. Giese has determined all indexes on the basis of the components wet weight.

Complex component indexes

The visceral mass of animals collected during November 1968; February, April, May, June, July, August, September, November, and December, 1969; and January, February, and March, 1970, were more completely dissected and more complex indexes were calculated. The female visceral mass was dissected into three distinct components: the ovary-digestive gland complex, the capsule-albumin gland complex, and the remaining visceral mass. The male visceral mass was dissected into two components: the testis-digestive gland complex and the remaining visceral mass. These components were stored in a similar manner as the visceral mass and foot until chemical analyses could be made.

Shell length-shell weight ratio

The ratio of shell length to shell weight was determined for each time that the population was sampled and a regression line constructed.

Statistical analyses

Body component indexes which were calculated each time the population was sampled and the egg capsule dry weights were analyzed as the mean plus and minus the confidence interval at the 95% level of significance. When a positive correlation (95% confidence level) existed between the natural logarithms of oxygen consumption, and snail dry weight, Bartlett's Best-Fit method was used to calculate the slope of the regression line, Y intercept, and 95% confidence limits of the slope (Simpson, Row and Lewontin, 1960). When no such correlation existed between the natural logarithms of oxygen consumption and dry weight, oxygen consumption was calculated on a per gram dry weight basis.

Orthogonal polynomials were fitted to the shell length-shell weight data by the least squares regression cubed method (Snedecor, 1956). The data was examined for a possible linear or curvilinear correlation of changes in the shell length-weight relationship with the reproductive cycle.

RESULTS

Field observations

Specimens of *T. lamellosa* were collected from among the barnacles, *Balanus cariosus*, except for the time when they were aggregated in breeding clumps. Most breeding clumps were more than five feet from the nearest barnacles and the animals apparently ceased feeding when aggregated.

Aggregation occurred after November 18 and copulation was observed between the aggregated animals on December 8, 1968. The same population was aggregated and copulating December 12, 1969. Spawning began within the aggregation between January 7 and 19, 1969 and around January 10, 1970. Animals had completed spawning and migrated to the barnacles by March 27, 1969 and by March 30, 1970.

The abundance of intertidal *Balanus cariosus* varied seasonally on Turn Island. Barnacles were abundant from September to November 1968 but barnacle density

was low from December 1968 to July 1969 with most of the barnacles being large and located high in the intertidal zone. A new barnacle settlement was first observed on July 14, 1969 and the young barnacles had grown considerably by August 17 when the last observation was made.

Respiratory rates

Oxygen consumption data for both sexes is given in Table I. There were times during the year when there was no correlation between the natural logarithms of oxygen consumption and snail dry weight. Both the absolute values of the

TABLE I
Seasonal changes in oxygen consumption of Thais lamellosa

Month	Correlation coefficient	95% signif.	Number of animals	Slope \pm 95% conf. interval	$\mu\text{l O}_2 \cdot \text{g}^{-1} \cdot \text{hr}^{-1}$
Males					
Oct. 68	0.715	S	12	0.65 ± 0.53	—
Nov. 68	0.517	S	16	0.75 ± 0.71	—
Dec. 68	0.376	NS	17	—	173 ± 36
Jan. 69	0.158	NS	37	—	139 ± 18
Feb. 69	0.361	S	36	0.19 ± 0.29	—
Mar. 69	0.776	S	26	1.02 ± 0.39	—
Apr. 69	0.189	NS	24	—	130 ± 20
May 69	0.327	NS	23	—	154 ± 24
June 69	0.457	S	28	0.48 ± 0.37	—
July 69	0.565	S	20	0.53 ± 0.36	—
Aug. 69	0.634	S	21	0.58 ± 0.37	—
Females					
Oct. 68	0.092	NS	17	—	155 ± 24
Nov. 68	0.572	S	25	0.42 ± 0.33	—
Dec. 68	0.227	NS	17	—	110 ± 23
Jan. 69	0.470	S	21	0.44 ± 0.35	—
Feb. 69	0.643	S	14	0.98 ± 0.75	—
Mar. 69	0.057	NS	24	—	85 ± 20
Apr. 69	0.710	S	24	0.71 ± 0.30	—
May 69	0.287	NS	27	—	124 ± 22
June 69	0.590	S	20	0.63 ± 0.42	—
July 69	0.654	S	31	0.47 ± 0.21	—
Aug. 69	0.558	S	20	0.63 ± 0.46	—

slopes and the confidence intervals about the mean values were quite variable.

In order to compare oxygen consumption data for all months, the oxygen consumption rate of standard animals with a dry tissue weight of 0.5 grams was determined for both sexes each month (Fig. 1). The oxygen consumption rate of males was highest during October, December, and March. It is interesting to note that males were normally actively copulating at the time of the December collection and had just begun feeding when collected in March. The oxygen consumption rate of females appeared to be more closely related to changes in water temperature than was the oxygen consumption rate of males.

Component indexes

Male body component indexes are given in Figure 2. There did not appear to be any seasonal periodicity in the size of the foot index. The male visceral mass index was largest in the fall and declined at a relatively constant rate throughout the period of aggregation. The visceral mass index declined from a December, 1968 value of 3.62 to 2.42 in March, 1969, and from 3.45 to 2.10 during the same time period of the 1969–1970 aggregation. This decline during aggregation was the result of two factors, starvation and copulation. The visceral mass index was smallest during the spring and summer months and was correlated with a lack of obtainable barnacles as prey. The visceral mass index increased 156% from an

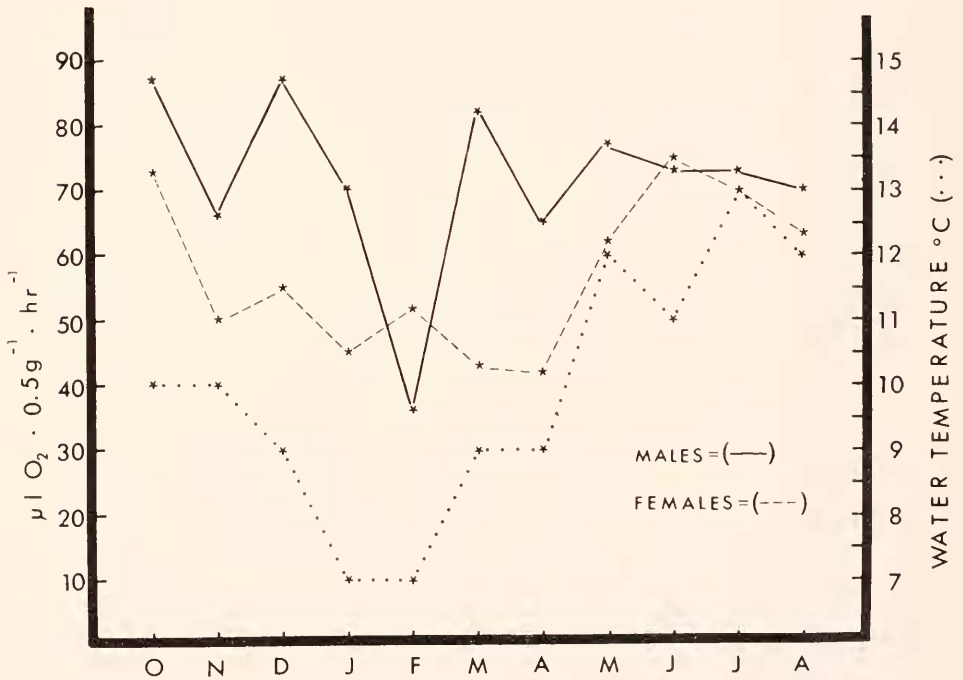


FIGURE 1. The average oxygen consumption rate of 0.5 gram tissue dry-weight male and female standard animals is given in microliters consumed per hour along the left Y axis. Ambient surface seawater temperature is given along the right Y axis.

August value of 2.74 to 4.27 in September, 1969. The body water index cycled in a manner similar to that of the visceral mass and the shell index cycled in an inverse relationship to changes in the visceral mass and body water indexes. The average index of each body component exhibited the following seasonal range: foot, 0.50–0.61; visceral mass, 1.96–5.01; body water, 9.64–12.98; and shell, 81.94–87.74.

Female body component indexes are given in Figure 3. The foot index did not appear to exhibit any seasonal periodicity. The female visceral mass index was

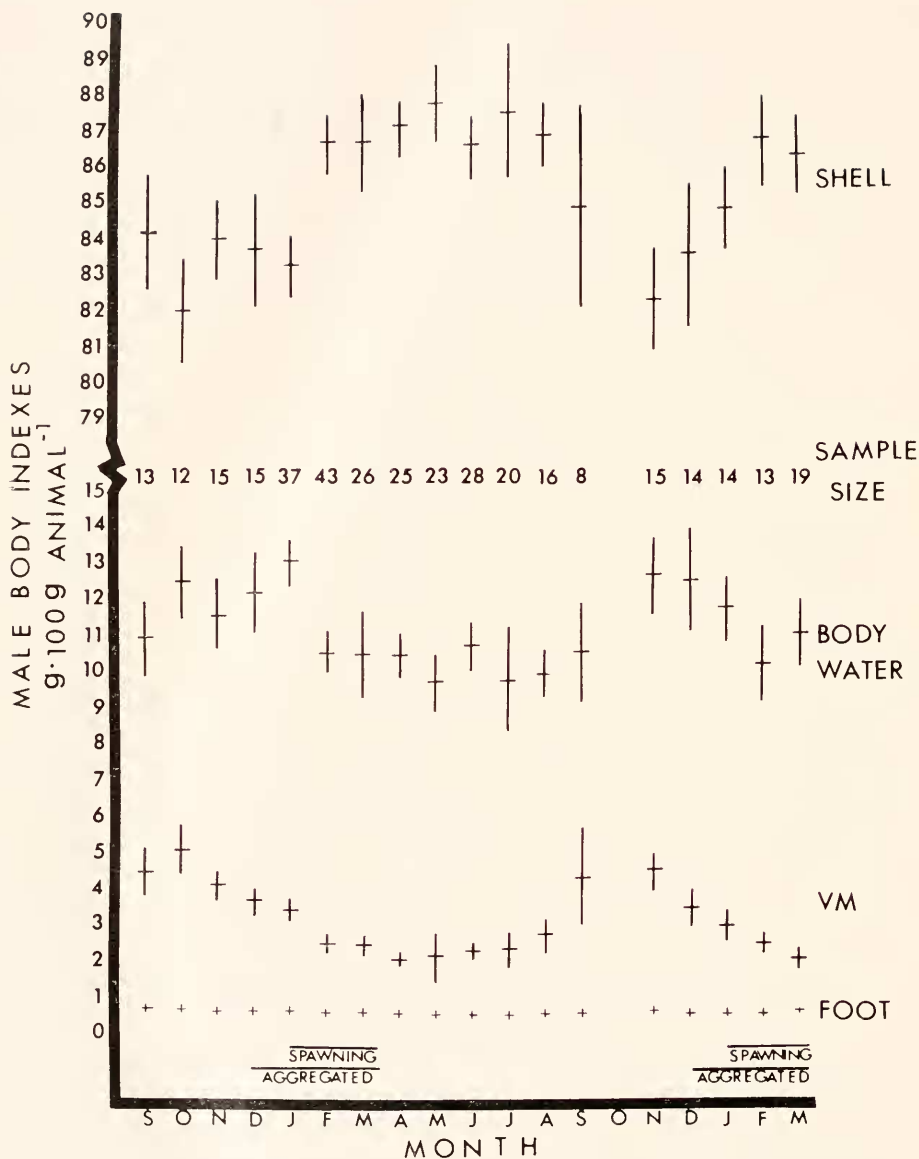


FIGURE 2. Male body component indexes are each represented by a cross. The horizontal line represents the mean and the vertical line the 95% confidence range about the mean.

largest during the fall and early winter with little difference in size occurring during these months. The visceral mass index declined from 4.84 to 3.01 between January and March, 1969 and from 4.53 to 2.04 between December, 1969 and March, 1970. Visceral mass material was lost during aggregation as a result of starvation and spawning by females. The visceral mass index continued to decline

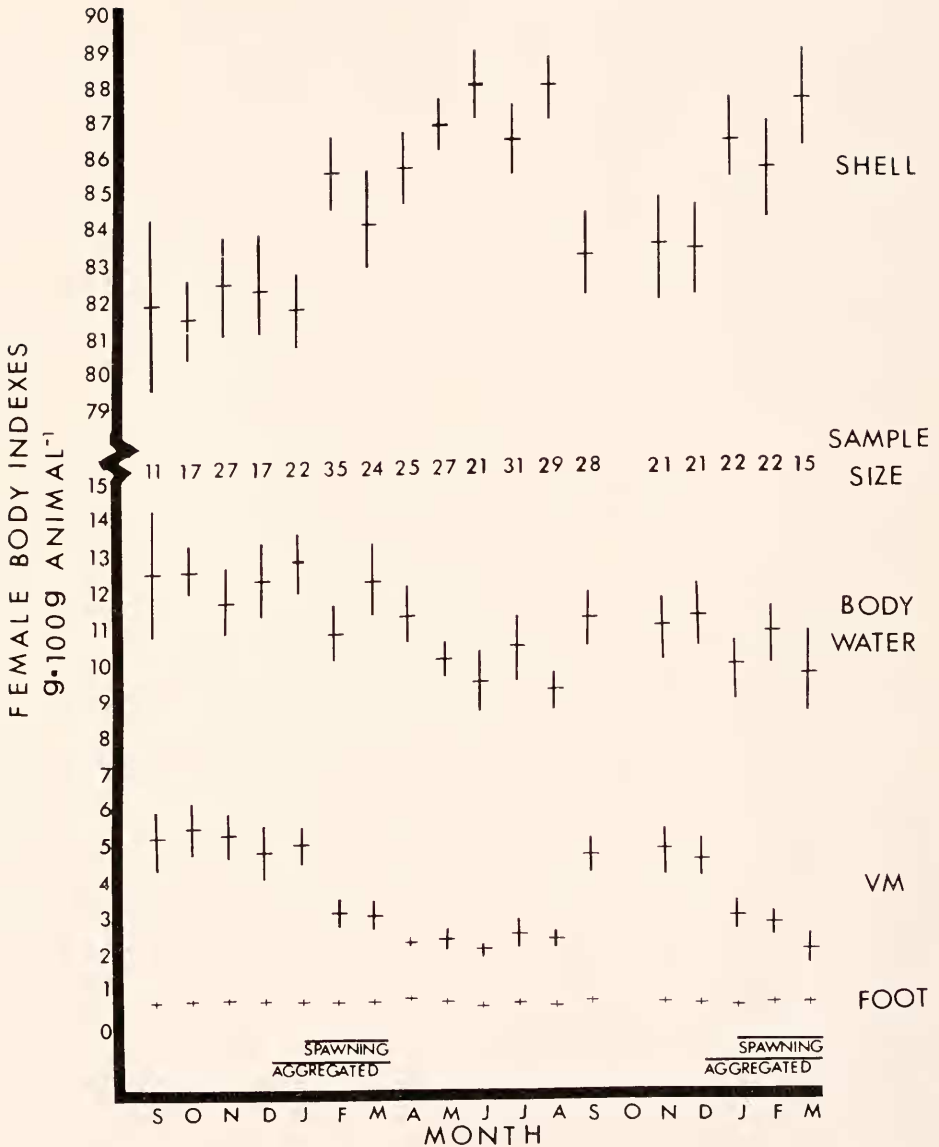


FIGURE 3. Female body component indexes are each represented by a cross. The horizontal line represents the mean and the vertical line the 95% confidence range about the mean.

from March to June, increased slightly in July and August, and doubled from 2.33 to 4.66 between August and September. The body water index cycled seasonally in a similar manner to that of the visceral mass index and the shell index cycled inversely. The average body component indexes of females exhibited the following seasonal range: foot, 0.50–0.66; visceral mass, 2.04–5.39; body water, 9.22–12.43; and shell, 81.49–88.01.

Complex component indexes

Data for the complex visceral mass component indexes of both sexes are given in Table II. There was little seasonal variation in the remaining visceral mass index of males. The testis-digestive gland index cycled seasonally in the same manner as the entire male visceral mass. Therefore, changes in the index of this complex component were responsible for the seasonal cycling of the male visceral mass. The average male complex visceral mass component indexes exhibited the following seasonal ranges: testis-digestive gland, 0.56–2.51; and remaining visceral mass, 1.29–1.98.

All three complex component indexes of the female visceral mass exhibited the same seasonal pattern, largest just prior to spawning and smallest during the late spring and summer. Seasonal changes in the remaining visceral mass index were not pronounced but the ovary-digestive gland complex and the capsule-

TABLE II
*Seasonal changes in the complex body component indexes
of *Thais lamellosa* (g./100g animal⁻¹)*

Month	Males			Females			
	Testes-DG complex	Remaining VM	Sample size	Ovary-DG complex	Caps.-Alb.G. complex	Remaining VM	Sample size
Nov.	2.46 ± 0.81*	1.85 ± 0.40	7	2.91 ± 0.77	0.94 ± 0.20	1.63 ± 0.24	12
Feb.	0.99 ± 0.50	1.45 ± 0.32	10	1.11 ± 0.45	0.54 ± 0.31	1.12 ± 0.16	9
April	0.56 ± 0.17	1.36 ± 0.11	12	0.76 ± 0.15	0.28 ± 0.06	1.37 ± 0.19	10
May	0.75 ± 0.22	1.42 ± 0.24	13	0.81 ± 0.24	0.39 ± 0.18	1.31 ± 0.19	10
June	0.66 ± 0.12	1.66 ± 0.12	10	0.65 ± 0.21	0.25 ± 0.07	1.14 ± 0.27	8
July	0.94 ± 0.48	1.62 ± 0.41	9	0.74 ± 0.27	0.20 ± 0.03	1.21 ± 0.25	11
Aug.	1.28 ± 0.25	1.53 ± 0.19	13	0.90 ± 0.20	0.23 ± 0.06	1.15 ± 0.14	12
Sept.	2.50 ± 0.97	1.77 ± 0.38	8	2.47 ± 0.34	0.61 ± 0.08	1.66 ± 0.13	28
Nov.	2.51 ± 0.36	1.98 ± 0.18	15	2.35 ± 0.43	0.87 ± 0.13	1.57 ± 0.17	21
Dec. 69	1.76 ± 0.36	1.77 ± 0.25	12	2.05 ± 0.28	1.04 ± 0.19	1.44 ± 0.12	21
Jan.	1.37 ± 0.16	1.47 ± 0.12	14	1.24 ± 0.26	0.60 ± 0.16	1.16 ± 0.10	22
Feb.	1.14 ± 0.18	1.40 ± 0.14	13	1.13 ± 0.26	0.51 ± 0.11	1.17 ± 0.10	23
March	0.73 ± 0.20	1.29 ± 0.18	19	0.68 ± 0.16	0.28 ± 0.14	1.08 ± 0.20	19

* Mean ± 95% confidence interval.

albumin gland complex indexes exhibited a distinct seasonal cycle. The average female complex visceral mass component indexes exhibited the following seasonal ranges: ovary-digestive gland, 0.65–2.91; capsule-albumin gland, 0.20–1.04; and remaining visceral mass, 1.08–1.66.

Biomass lost per female during spawning

One can estimate the percentage of visceral mass size lost by females during spawning which was deposited as egg capsules. The average dry weight of 78 freshly laid egg capsules was 4.6 ± 0.6 mg. Spight's (1972) estimates of 36.2 capsules laid per female during the 1969 spawning period and 48.3 capsules laid during 1970 were multiplied by the average capsule dry weight to determine the

total capsule weight lost per female during spawning. The average entire weight of the 420 females examined during this study was 11.3208 grams (range—3.9090 to 30.3442 g) and the average length was 40.9 mm (range—32.0 to 56.0 mm). Visceral mass biomass lost during spawning was adjusted to the amount lost by an 11.3208 gram female from January to March 1969 and from December 1969 to March 1970. The difference between the total visceral mass biomass lost during the spawning period and the amount deposited as egg capsules can be attributed to female respiration. These calculations are presented in Table III.

More biomass was lost from the female visceral mass during 1970 than in 1969. Spight (1972) reported a higher capsule production per female in 1970 than in 1969. Most of the biomass lost from the female visceral mass during both of the spawning periods was deposited as capsular material. The 1969 spawning period was estimated to be 82 days and the 1970 period 78 days.

Shell length—shell weight relationship

Because the shell comprises a large percentage of the body of *Thais lamellosa*, the possibility of seasonal changes in the shell length—weight ratio was investigated.

TABLE III

Biomass lost per gram Thais lamellosa female during 78–82 day spawning period

Capsules laid per female*	Dry weight per capsule (mg)	Dry weight lost as spawn (mg)	Dry weight lost from the VM** (mg)	Per cent VM dry weight lost as spawn	Per cent VM metabolized as tissue
1968–69					
36.2	4.6	167	207	81	19
1969–70					
48.3	4.6	218	282	77	23

* From Spight (1972).

** Visceral mass size lost during the spawning period in a 100 gram female was reduced to the amount lost by an 11.3208 gram female and expressed in milligrams.

Significant seasonal changes in the relationship between shell length and weight would be indicative of a variable pattern of shell deposition and such information would be valuable to the explanation of seasonal changes in the other body component indexes.

There was no linear or curvilinear correlation between the shell length—shell weight relationship and the monthly sampling dates for the population. Therefore, it does not appear likely that seasonal changes in the rate of shell deposition are responsible for the reproductive cycle periodicity of the body component indexes. The seasonal changes which occur in the shell index of both sexes are simply a reflection of changes occurring in the magnitude of the other indexes.

DISCUSSION

Thais lamellosa differs in several important ways from the other prosobranchs for which body component indexes are available. *Haliotis cracherodii* and *M.*

crenulata are herbivores whereas *P. lewisii* and *T. lamellosa* are carnivores. *Haliotis cracherodii* and *M. crenulata* are broadcast fertilizers (Webber and Giese, 1969; Morton, 1958). *P. lewisii* produces a sand collar composed of sand mingled with a gelatinous secretion and containing spaces occupied by eggs (Hyman, 1967), and *T. lamellosa* deposits fertilized eggs in a well developed egg capsule.

The foot comprises the predominant body component of *H. cracherodii*, *M. crenulata*, and *P. lewisii* but is a minor component of *T. lamellosa*. Relative size differences of the foot can be best explained by considering the ecological niche of each species. The foot of *H. cracherodii* and *M. crenulata* is modified into a broad flat sole used for creeping over the rocks from which the snails rasp a diatom film. The pedal lobes of the foot of *P. lewisii* can be expanded to completely cover its shell by the animal pumping seawater into the foot's intersitial spaces. Expansion of the pedal lobes presumably protects the shell from the abrasive action of the sand or mud through which the species crawls (Hyman, 1967). In contrast to the other three species, the foot of *T. lamellosa* is unspecialized and is used to attach the species to rocks and prey.

The shell index of *T. lamellosa* is much larger than that of the other three species. Its index ranges from 81.49 to 88.01 seasonally as compared to indexes of 61.6 for *P. lewisii*, 37 for *H. cracherodii*, and 7.4 for *M. crenulata*.

There is much inter-population variability in the shell morphology of *T. lamellosa* (Kincaid, 1957). Much of the variability is undoubtedly genetic in that no planktonic larvae is produced by the species and genetic exchange between populations is rare. In addition, Malone and Dodd (1967) have shown the calcification rate of *Mytilus edulis* to vary directly with salinity and temperature. The shell indexes of a population of *T. lamellosa* from Saint Therese, Alaska ranged from 72.56 to 83.13 (Stickle, unpublished data) as compared to the 81.49 to 88.01 range from the Turn Island, Washington population. The Saint Therese population is faced with colder winters and less saline water during the summer months than the Turn Island population. Environmental conditions are therefore more favorable for shell calcification at Turn Island, Washington than at Saint Therese, Alaska.

Reproductive tract complexity correlates well with the evolutionary status of the species within the subclass Prosobranchiata. Morton (1958) states that archaeogastropods and mesogastropods deposit less extraembryonic material around their gametes than neogastropods. The oviducts of the archaeogastropods, *H. cracherodii* and *M. crenulata* is undifferentiated, that of the mesogastropod *P. lewisii* is somewhat developed, and that of *T. lamellosa* is very well developed.

The reproductive tract morphology of *T. lamellosa* has not been described in the literature but it appears to be similar to that of *T.* (= *Nucella*) *lapillus* (Fretter, 1941; Fretter and Graham, 1962), *T. emarginata*, and *T. canaliculata* (Houston, 1971). The prostate gland is the only major accessory structure of the male and was included in the remaining visceral mass component of this study. The female capsule and albumin glands produce all of the extraembryonic material secreted around *T. lamellosa's* eggs. The albumin gland coats the eggs with a layer of albumin and the capsule gland produces the egg capsule.

It is metabolically expensive for animals to secrete extraembryonic material around gametes. The metabolic expense of producing extraembryonic material is balanced by the production of fewer eggs than occurs in broadcast fertilizers. The female capsule-albumin gland complex declined from 17% to 12% of the visceral mass size during spawning in 1969 and from 26% to 14% in 1970. If body components are adjusted to an 11.3208 gram animal, biomass lost from the capsule-albumin gland complex during spawning would account for 45% of the visceral mass biomass deposited as spawn in 1969 and 39% in 1970. It is also assumed that no biomass was transferred to the capsule-albumin gland complex from other body components. Lawrence, Lawrence, and Giese (1965), however, found a reciprocal relationship to exist between the digestive gland and glandular oviduct indexes of the amphineuran *Katherina tunicata*. An inverse relationship of such nature suggests nutrient transfer from the digestive gland to the oviduct during gametogenesis.

The gonad-digestive gland complex was probably the energy source for the production of gametes and maintenance of body functions during aggregation and spawning. Unfortunately it was impossible to separate the gonad and digestive gland tissue of *T. lamellosa*. Webber (1970) found no seasonal change in the digestive gland index of *H. cracherodii*.

The remaining visceral mass index of *T. lamellosa* does not appear to exhibit a seasonal cycle. However, this is not surprising since it contains such organs as the heart, kidney, gills, mantle, salivary glands, *etc.*, which have never been shown to be nutrient depots.

Seasonal differences in food availability can effect a species' pattern of nutrient deposition. If prey were abundant year around, less food would have to be stored prior to the initiation of gametogenesis.

Webber (1970) suggested that seasonal differences in the feeding rate of *H. cracherodii* may have been responsible for a different relationship between the foot and gonad indexes during two periods of gonad growth. Foot size decreased during the first (larger) period of gonad growth but increased during the second (smaller) period which occurred just after spawning. The abalone population was observed to be feeding more during the postspawning period of gonad growth than at any other time of the reproductive cycle. Webber felt that there was sufficient energy intake during the postspawning period of gonad growth to satisfy energy demands for abalone maintenance, growth, and gonad maturation but that insufficient energy was ingested to satisfy all three energetic demands during the prespawning gonad growth phase.

Barnacle density and intertidal position probably affected changes in *T. lamellosa's* body component indexes. The intertidal barnacles remaining at the conclusion of the snails' 1969 spawning period were very large and located near the high tide line. Both barnacle size and intertidal position would make it difficult for *T. lamellosa* to prey upon them. Emlen (1966) has shown *T. lamellosa* to most efficiently eat barnacles of much smaller size than those found at Turn Island in March 1969. In addition, the higher a barnacle is in the intertidal zone, the less time it is submerged and *T. lamellosa* only drills barnacles while submerged.

A new barnacle settlement was not observed until July 14, 1969. This lack of prey could explain the rather constant visceral mass index between March and August. The young barnacles had grown considerably by August 17, 1969. The tremendous increase in the visceral mass indexes of both snail sexes between August and September can probably be explained by the fact that the young barnacles had grown to a size where they could be efficiently preyed upon by adult *T. lamellosa*.

A successful barnacle settlement is probably reflected the following year by an increased capsule production by female *T. lamellosa*. Spight (1972) reported the 1969 barnacle settlement to be the most successful in years and reported a higher capsule production by female snails in 1969-1970 than had occurred in 1969.

Aggregation was extremely demanding on adults of *T. lamellosa* which were starving and depositing 77-81% of their prespawning visceral mass size as spawn during that three to four month period. Pearce and Thorson (1967) indicated that females of *Neptunca antiqua* became exhausted following spawning and starving. Eight of nine females observed during spawning in the laboratory died within three months after spawning. Stickle (1971) has shown that adult specimens of *T. lamellosa* could be starved for an additional 91 days after the completion of spawning before 50% of the snails died. Specimens of *T. lamellosa* were capable of an extremely protracted period of starvation at ambient sea water temperature (Stickle and Duerr, 1970; Stickle, 1971). Resistance to starvation allows the species to survive periods of time when food is scarce.

There appeared to be no compensation in *T. lamellosa's* oxygen consumption rate. Less metabolic substrate was therefore utilized by females for body maintenance during aggregation in the winter months than would have occurred if thermal acclimation existed. However, the oxygen consumption rate of males increased significantly at the beginning and conclusion of aggregation. The increased oxygen consumption rate at the beginning of aggregation can be explained by the fact that male copulatory activity is most pronounced during early aggregation and declines with its duration (Spight, 1972). Metabolic conversions involved in sperm production and copulatory activity were probably quite high at the beginning of the aggregation. The increased oxygen consumption rate at the conclusion of aggregation may have been due to an increased rate of lipogenesis. The lipid level and content of males increased from February to March although the increase was not statistically significant (Stickle, unpublished data). However, male snails collected at Turn Island on February 25, 1969 and starved for 91 days at ambient water temperatures synthesized significant amounts of lipid.

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SUMMARY

1. Body component indexes of *Thais lamellosa* were determined over a period of 19 months. Snails were separated into shell, body water, foot, and the visceral mass including its more complex components consisting of the gonad-digestive gland, remaining visceral mass and the female capsule-albumin gland. Indexes were expressed as grams of the component \times grams of the entire animal⁻¹ \times 100. Spawn was collected and weighed. The rate of oxygen consumption was determined for the first year of the study.

2. The body water, visceral mass, gonad-digestive gland, capsule-albumin gland, and female remaining visceral mass indexes exhibited a seasonal cycle of being largest just prior to population aggregation in November, declining during aggregation and remaining low during the summer months. These indexes greatly increased between August and September and remained high until the next population aggregation. The shell index cycled in an inverse pattern to that of the others, merely reflecting changes in the magnitude of the sum total of the other indexes.

3. Aggregation is demanding upon *T. lamellosa* because it is accompanied by spawning and starvation. Spawn accounted for 77–81% of the size of the visceral mass lost during aggregation with the remainder being lost through respiration. Capsule-albumin gland material accounted for 39–45% of the biomass lost from the visceral mass as spawn. The production of extraembryonic material is metabolically demanding of adult snails.

4. The availability of barnacles of optimum size and distribution for predation by *Thais* is integrally related to the snail's pattern of nutrient deposition. Barnacles were unavailable for efficient predation from November–August. The increase in the visceral mass, gonad-digestive gland, and the capsule-albumin gland indexes between August and September was probably related to the presence of barnacles of optimum size for predation.

5. The rate of oxygen consumption of both sexes was directly related to water temperature with the male rate being higher than expected from the water temperature at the beginning and end of aggregation.

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